

DITERPENOID ALKALOID CONCENTRATION IN TALL LARKSPUR PLANTS DAMAGED BY LARKSPUR MIRID

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Abstract—Tall larkspur (*Delphinium barbeyi*) is a serious poisonous plant threat to cattle on mountain rangelands. The larkspur mirid [*Hopplomachus affiguratus*] has been proposed as a biological tool to damage tall larkspur in an effort to deter grazing by cattle and thus prevent poisoning. Preliminary data suggested that it may also reduce toxic alkaloid levels. The objective of this study was to determine if damage caused by the larkspur mirid would reduce toxic alkaloid concentration. Larkspur mirids were collected in the field in 1992 and placed on potted plants in the greenhouse. The resulting mirid-damaged leaves were lower in toxic alkaloids than leaves from uninfested plants. In the 1995 field study, toxic and total norditerpenoid alkaloid concentrations were measured in two larkspur populations having established mirid populations and in two newly infested larkspur populations. In the 1996 field study, three widely separated larkspur populations infested with mirids were sampled. Mirid-damaged leaves were lower in toxic alkaloids in both years, but there were no differences in flowering heads. However, only at Yampa, Colorado, did mirids reduce toxic alkaloids to levels that would not pose a threat to cattle. There was no difference in toxic or total alkaloid concentration between larkspur populations with long-term mirid infestations compared to newly infested plants. The plant-to-plant variability in alkaloid concentration was greater than differences due to mirids.

Key Words—Biological control, *Hopplomachus affiguratus*, Heteroptera, Miridae, cattle poisoning, *Delphinium barbeyi*, norditerpenoid alkaloids, methyllycaconitine.

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INTRODUCTION

Tall larkspur (*Delphinium barbeyi*) is a serious poisonous plant threat to cattle on mountain rangelands. The larkspur mirid [*Hopplomachus affiguratus* (Heteroptera: Miridae)] is a native insect that is host-specific to tall larkspur (Fitz, 1972; Uhler, 1895). It is a sucking insect that extracts cell solubles from immature, rapidly growing plant parts. The insects concentrate on flowering racemes, causing the buds to abort, and also damage the leaves, which first appear mottled, then desiccate and senesce. These are the larkspur plant parts normally preferred by cattle (Pfister et al., 1988a) and cattle will not graze mirid-damage larkspur plants (Ralphs et al., 1997a). Thus, the larkspur mirid has been proposed as a biological tool to damage tall larkspur in an effort to deter grazing by cattle and thus prevent poisoning.

Preliminary data indicate that toxic alkaloid concentration was lower in mirid-damaged larkspur plants than in undamaged plants (Ralphs unpublished data). Therefore, the larkspur mirid may have the potential to reduce larkspur toxicity, as well as its palatability. The objectives of this study were to determine the influence of mirid damage on toxic and total alkaloid concentration in tall larkspur and to determine if long-term mirid infestations suppressed alkaloid levels in larkspur populations compared to newly infested plants.

METHODS AND MATERIALS

Larkspur Alkaloids

The toxic compounds in larkspurs have been identified as norditerpenoid alkaloids (Figure 1). Alkaloids that contain the *N*-(methylsuccinimido) anthranilic ester group (referred to as MSAL alkaloids) are the most toxic (Manners et al., 1995), with methyllycaconitine (MLA) and 14-deacetylnudicauline (DAN) being the two most prominent toxic alkaloids in tall larkspur. In the preliminary greenhouse study, concentration of MLA, the dominant toxic alkaloid, was measured by high-pressure liquid chromatography (HPLC) following extraction in ethanol and chloroform (Manners and Pfister, 1993). The MSAL fraction (referred to as toxic alkaloids) and total alkaloid concentration in the 1995 and 1996 studies were analyzed by Fourier-transformed infrared spectroscopy (FTIR) (Gardner et al., 1997). The alkaloids were extracted in chloroform and 1% H₂SO₄, and IR spectra were collected with a Nicolet Magna 550 FT-IR spectrometer (Nicolet Instrument Corp., Madison, Wisconsin).

Preliminary Study

A dense population of the larkspur mirid exists in a tall larkspur patch near Ferron Reservoir, 45 km west of Ferron in east-central Utah. In 1992, a large

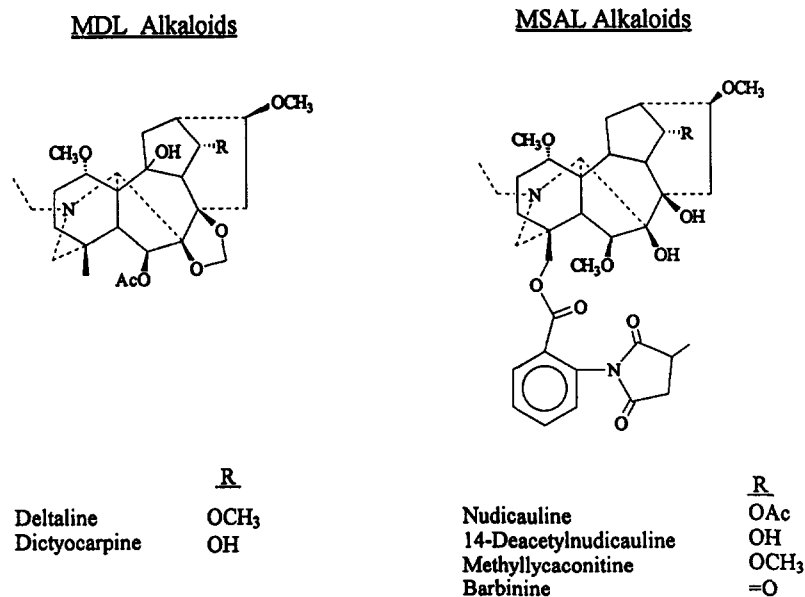


FIG. 1. Norditerpenoid alkaloids in tall larkspur. The two major classes of alkaloids are methylenedioxylycoctonine (MDL) and *N*-(methysuccinimido)anthranoyllycoctonine (MSAL) alkaloids.

number of live nymphs and adult mirids were collected from the field and transferred to six potted larkspur plants in our greenhouse in Logan. After three weeks, leaves from these six plants were harvested, along with leaves from six control plants. All samples were dried in a forced air oven at 60°C, ground in a Wiley mill to pass through a 1-mm screen, and analyzed for MLA by HPLC.

1995 Study

The study was conducted on the Wasatch Plateau 45 km west of Ferron in central Utah. Four sites were selected in the subalpine zone (3000–3300 m elevation). The vegetation community consisted of scattered subalpine fir stands interspersed in the tall forb plant community dominated by tall larkspur, western cone flower (*Rudbeckia occidentalis*), sweet cicely (*Osmorhiza occidentalis*), and mountain brome (*Bromus carinatus*). Tall larkspur is a large robust native perennial forb. It has an average of 40 stems/plant (ranging up to 150 stems/plant) and grows to a height of 1 m in this area. It generally occurs in patches associated with snow drifts. The growing season is short at this elevation; growth begins as the snow melts in mid-June, and freezing temperatures curtail growth in early September.

The objective of this study was to compare the alkaloid concentration in mirid-damaged and undamaged parts of plants from larkspur populations where mirids have been abundant in the past, compared to larkspur populations in which the mirids were recently transplanted. Two sites were selected in each population type.

Existing Mirid Population. The first site was 3 km west of Ferron Reservoir. We first discovered the larkspur mirid in this area in 1989 in a 3-ha larkspur patch and have observed significant mirid damage each year. We estimated the mirid density at about 10,000 mirids per plant. There was an average of 90 mirids/leaf on the younger leaves on the upper half of the stem (6 leaves/stem), on about half the stems of each plant (20 stems/plant) at a given time. The mirids did not uniformly cover each plant. They were concentrated on the south-east quarter of the plant at the beginning of the season (perhaps due to the orientation of the morning sun), then spread throughout the plant as the season progressed. About half of each plant was damaged at the time the samples were harvested.

The second site was on 6-Mile Bench about 12 km north west of the first site. We transplanted the larkspur mirid to this location in 1993, and its population increased and spread throughout the 0.5-ha patch. Larkspur was in the early flower stage at Ferron Reservoir (0.9 m tall), and the early bud stage at 6-Mile (0.6 m tall), on August 8, 1995, when the samples were harvested.

There is a tremendous amount of variability in toxic alkaloid concentration among larkspur plants (Manners and Pfister, 1996). Therefore, samples were taken from a plant with both mirid-damaged and undamaged leaves and flowering heads. We randomly selected 10 larkspur plants at each location that had significant mirid damage. We selected about 15 flowering racemes (heads) and 50 leaves that were damaged, and the same number of heads and leaves without mirid damage from each plant. The respective samples were placed in paper bags, transported to our lab, and processed as described above and analyzed for total and toxic alkaloids by FTIR.

Transplant Population. Nymphs in the second to fourth instar were taken from the Ferron Reservoir population and transplanted at two uninfested larkspur patches in Duck Fork (4 km north) and 12-Mile Canyon (8 km west). Mirids were gently shaken from the larkspur plants into an insect sweep net, then were placed in large white garbage bags containing several larkspur stems to prevent bunching up. They were placed on the new plants within an hour. Ten robust plants were selected at each location, and each plant was divided in half using a nylon mesh screen (1-mm openings). Sections of screen (0.9 m wide and 0.6 m tall) were stapled to 1.2-m surveyor's stakes, which were driven into the ground splitting the foliage of each plant in half. The screens were oriented east to west, and the mirids were randomly placed on either the south or north side of the screen. From 500 to 1000 nymphs were placed on each plant.

The nymphs were transplanted on August 8, and the plant parts were harvested on August 25. Undamaged plants were in the full flower stage at Duck Fork and in the bud elongation stage at 12-Mile when harvested. Larkspur heads and leaves from the mirid-damaged and undamaged portions of the plants were harvested and processed, and alkaloid concentration was measured by FTIR. Some of the heavily damaged leaves on the mirid side of the screen were totally desiccated. These leaves were kept separate and analyzed as a third type of leaf in this study (undamaged, mirid-damaged, desiccated).

The extent of mirid damage was estimated on these recently infested plants. A visual estimate was made of the percentage of desiccated leaves and the percentage of leaf biomass damaged. The numbers of aborted heads and normal heads on each side of the screen were counted, and the percentage of aborted heads was calculated.

1996 Study

The objective of this study was to compare the toxic and total alkaloid concentration in mirid-damaged and undamaged plant parts in larkspur populations over a wide geographical area. Larkspur samples were collected from mirid-damaged larkspur patches on the Wasatch Plateau in central Utah 22 km east of Mayfield, on the Fishlake National Forest in south-central Utah 46 km east of Salina, and on the Routt National Forest 20 km west of Yampa on the western slope of Colorado.

The Mayfield site is in the same general area as the 1995 study, but on the west slope of the mountain. The Salina site was 50 km south at a similar elevation and plant community. The Yampa site was in an open park within the aspen vegetation zone at 2500 m elevation. Dominant species included tall larkspur, elderberry (*Sambucus racemosa*), saw groundsel (*Senecio serra*), and mountain brome (*Bromus carinatus*).

Mirid-damaged and undamaged leaves were taken from the same plant at Mayfield and Salina. Ten plants were randomly selected at each site. From 30 to 50 mirid-damaged and undamaged leaves were taken from the upper half of each plant at both sites, and 10–15 damaged and undamaged heads were taken from each plant at the Mayfield site. There were few undamaged heads at the Salina site; therefore only leaf samples were taken. At Yampa, infested plants were uniformly damaged (there were no undamaged plant parts on infested plants); therefore leaves and heads were harvested from six mirid-damaged and six undamaged larkspur plants. Alkaloids were measured by FTIR.

Nutrient Quality. Nutrient quality of mirid-damaged and undamaged leaves was also measured. Nitrogen was measured by an automated combustion method (Sweeney, 1989) that quantifies total N by thermal conductivity. Total N was multiplied by 6.25 to obtain crude protein (CP). Neutral detergent fiber (NDF)

was measured by the filter bag technique (Komarek et al., 1994) using standard NDF solution. NDF is a measure of cell walls, with its inverse being soluble cell contents. Sugar analysis was attempted, but results were inconclusive due to the large losses of soluble carbohydrate in the drying method.

Statistical Analysis of Data

The 1992 data from the preliminary greenhouse study were analyzed by one-way analysis of variance (ANOVA) with comparison of toxic alkaloid concentration in mirid-damaged and undamaged leaves. The two field studies were first analyzed singly, then combined and analyzed together in a large general linear model (GLM).

In the 1995 study, the concentration of toxic and total alkaloids in larkspur plant parts were compared between the existing mirid populations and transplanted populations by ANOVA. Differences between populations were tested by the site (within population) factor. The plant part and part \times population interaction was tested by the part \times plant (within population) factor, and the mirid-damage and two- and three-way interactions with population and parts were tested by the residual error. Differences between populations (existing vs. transplanted mirids) and sites were somewhat confounded with differences in time of harvest and phenological growth stages of larkspur. Therefore, the difference in toxic and total alkaloids at each site was tested by paired t tests, comparing mirid-damaged and undamaged leaves and heads on the same plant.

In the 1996 study, the concentration of toxic and total alkaloids in mirid-damaged and undamaged plants was compared among locations and plant parts by GLM.

The alkaloid data from the two field studies were then combined and analyzed together in a large GLM model. Sites were tested by the plant (within site) factor. Mirid-damage and the site \times damaged factors were tested by the residual error. There was a significant site \times mirid-damage interaction ($P < 0.05$) for both leaves and heads. Therefore, the difference in toxic and total alkaloids in mirid-damage and undamaged parts from the same plant at each site (except Yampa) were tested by paired t tests. Yampa samples were compared by one-way ANOVA.

The variability in alkaloid concentration due to the mirid damage and the inherent variability between plants was partitioned within each population and site by a randomized block design ANOVA. The sum of squares for treatment (mirid-damaged vs. undamaged) and the sum of squares for block (individual plants) was divided by the total sum of squares to determine the proportion of variability due to the mirid and the proportion due to differences among individual plants (Coleman et al., 1987).

Nutrient components (CP and NDF) of mirid-damaged and undamaged larkspur leaves in the 1996 study were analyzed by GLM in a 2×3 factorial design. Mirid damage was a fixed factor and was tested by the residual error. The three sites were random factors and were tested by the damage by location interaction.

RESULTS AND DISCUSSION

Mirid-Damaged vs. Undamaged Plants in 1992, 1995, and 1996 Studies

Mirid-damaged larkspur plants in the 1992 greenhouse study were lower in the toxic alkaloid MLA than the undamaged control plants ($P = 0.07$, Table 1). The levels of MLA in the potted plants in the greenhouse are typically lower than plants in their natural populations in the field (Ralphs et al., 1997b).

Mirid-damaged leaves were lower in toxic alkaloids in the combined 1995 and 1996 data set than control leaves (5.0 vs. 6.0 mg/g, $P < 0.001$, Table 1). Total alkaloids in mirid-damaged leaves were also lower in the 1996 study (12.8 vs. 15.1 mg/kg, $P < 0.001$), but were similar in 1995 to control leaves (27.0 vs. 26.2 mg/kg, $P = 0.17$). There were few differences in toxic alkaloids in flowering heads in either year.

There were large differences in both toxic and total alkaloids between larkspur plant parts in 1995 ($P < 0.001$). Leaves contained 2.4 times more toxic alkaloids than flowering heads and 75% more total alkaloids. This is contrary to the seasonal trend in alkaloid levels in which the flowering heads and pods are generally higher in toxic alkaloids (Ralphs et al., 1997d) and total alkaloids (Ralphs et al., 1988) than leaves. There were no differences between leaves and flowering heads in the 1996 study.

There were differences in both toxic and total alkaloids between sites when averaged over mirid-damaged and undamaged plants in the 1995 study ($P < 0.05$). The 6-Mile site had higher toxic and total alkaloids in larkspur leaves and higher toxic alkaloids in heads than the other sites (Table 1). The 12-Mile site had higher total alkaloids in larkspur heads. This was probably due to differences in phenological development at the time of harvest. Both toxic and total alkaloid concentration in tall larkspur are highest in early growth and decline as the plants mature (Manners et al., 1993; Ralphs et al., 1997d). Plants harvested at 6-Mile were in the earliest phenological growth stage (early bud), and plants at 12-Mile were in the bud elongation stage when harvested, compared to the early and full flower stage at Ferron Reservoir and Duck Fork, respectively.

There were differences between locations in the 1996 study. Larkspur heads

TABLE 1. TOXIC AND TOTAL ALKALOID CONCENTRATION IN MIRID-DAMAGED AND UNDAMAGED PLANT PARTS IN EXISTING AND TRANSPLANTED MIRID POPULATIONS AT 4 LOCATIONS IN 1995 AND EXISTING MIRID POPULATIONS AT 3 LOCATIONS IN 1996

Part	Year	Mirid population	Site	Conc mg/g \pm SE			
				Toxic Alkaloids		Total Alkaloids	
				Mirid-damaged	Undamaged	Mirid-damaged	Undamaged
Leaf	1992	Transplant	Greenhouse	0.2 \pm 0.1b*	0.8 \pm 0.3a		
	1995	Existing	Ferron	5.5 \pm 0.6 [†]	6.5 \pm 0.7	22.7 \pm 1.6	22.5 \pm 1.4
			6-Mile	7.5 \pm 0.8	7.1 \pm 1.0	31.2 \pm 2.8	29.4 \pm 3.1
		Transplant	12-Mile	4.6 \pm 0.7 [†]	5.2 \pm 0.7	26.5 \pm 1.4	25.3 \pm 0.9
			Duck Fork	5.2 \pm 0.8 [†]	6.4 \pm 0.9	27.6 \pm 1.9	27.7 \pm 2.1
	1996	Existing	Mayfield	4.5 \pm 0.6 [†]	6.0 \pm 0.8	19.5 \pm 1.6	20.7 \pm 1.7
			Salina	5.0 \pm 0.6 [†]	6.0 \pm 0.7	11.1 \pm 1.1 [†]	14.1 \pm 1.3
			Yampa	1.5 \pm 0.1b	4.2 \pm 0.5a	4.6 \pm 0.4b	7.3 \pm 0.1a
			Mean	5.0 \pm 0.4b	6.0 \pm 0.3a	21.4 \pm 1.2a	21.8 \pm 1.1a
Head	1995	Existing	Ferron	2.4 \pm 0.3	2.2 \pm 0.2	14.1 \pm 1.4	12.0 \pm 1.0
			6-Mile	3.3 \pm 0.4	3.2 \pm 0.5	16.7 \pm 1.6	14.9 \pm 1.6
		Transplant	12-Mile	2.1 \pm 0.2	2.3 \pm 0.2	18.4 \pm 1.1	16.7 \pm 0.7
			Duck Fork	2.9 \pm 0.3 [†]	2.1 \pm 0.2	16.0 \pm 0.8 [†]	12.6 \pm 0.7
	1996	Existing	Mayfield	4.1 \pm 0.4	4.2 \pm 0.5	15.3 \pm 1.0 [†]	18.4 \pm 0.8
			Yampa	2.2 \pm 0.3b	3.5 \pm 0.3a	10.8 \pm 0.3	8.1 \pm 0.7
			Mean	2.9 \pm 0.2a	2.9 \pm 0.2a	15.6 \pm 0.6a	14.7 \pm 0.6a

* Means followed by different letters are significantly different ($P < 0.05$), as determined by ANOVA.

[†] Difference between mirid-damaged and undamaged parts of the same plant are significant ($P < 0.05$) as determined by paired t test.

TABLE 2. CRUDE PROTEIN AND NEUTRAL DETERGENT FIBER (NDF) IN MIRID-DAMAGED AND UNDAMAGED LARKSPUR LEAVES FROM 1996 STUDY

Site	N	Crude Protein (% \pm SE)		NDF (% \pm SE)	
		Mirid-damaged	Undamaged	Mirid-damaged	Undamaged
Mayfield	10	16.4 \pm 0.7	18.9 \pm 0.8	23.0 \pm 0.5	19.7 \pm 0.7
Salina	10	14.4 \pm 0.4	16.7 \pm 0.4	20.4 \pm 0.4	17.1 \pm 0.6
Yampa	6	15.5 \pm 0.4	16.4 \pm 0.2	21.0 \pm 2.5	17.2 \pm 1.1
Mean		15.4 \pm 0.4b*	17.4 \pm 0.4a	21.6 \pm 0.4a	18.1 \pm 0.5b

* Means followed by different letters are significantly different at $P < 0.05$.

and leaves at Yampa, Colorado were lowest in toxic and total alkaloids, and total alkaloids at Salina were intermediate (Table 2). Larkspur was in the full flower stage of development at all three locations when harvested. We have no explanation for why larkspur plants at Yampa were lower in alkaloids than larkspur plants at the other locations.

Existing vs. Newly Transplanted Mirid Populations, 1995

In most of our transplant studies, mirids survived, but did not increase in density or spread throughout the patch. We hypothesized that the mirid population may need to reach a critical threshold to suppress the chemical defenses of larkspur before the mirid population could continue to grow. However, there was no difference in toxic or total alkaloids in larkspur plants from existing mirid populations compared to those plants onto which the mirids were recently transplanted ($P > 0.30$). Neither was there a population \times mirid-damage interaction ($P > 0.62$), which suggests that mirids did not suppress alkaloids to a greater degree in the existing population, compared to the newly transplanted population. Therefore, norditerpenoid alkaloids may not constitute chemical defenses against the mirids.

In the transplant populations, mirids caused substantial damage on the halves of plants on which they were placed ($P < 0.01$). On the mirid-damaged halves, 29% of the leaves were desiccated, 50% of the remaining leaf biomass was damaged, and 82% of the flowering heads aborted. In contrast, the undamaged halves had no desiccated leaves, only 12% of the leaf biomass was damaged, and 5% of the heads aborted from other natural causes.

This high level of damage inflicted by mirids on larkspur plants may affect the reproductive performance and long-term vigor of larkspur populations. The mirids caused the flowers to abort, thus preventing seed production. However, tall larkspur is not dependent upon seed production to maintain its population. It is a long-lived perennial forb, living up to 75 years (Cronin and Nielsen, 1979). However, leaf damage may reduce the vigor of larkspur plants, thus allowing other plants a competitive ecological advantage, and subsequently reduce larkspur's dominance in the plant community over time.

The alkaloid content of the heavily damaged leaves that had senesced remained quite high. These leaves were brown, withered, and desiccated. The toxic alkaloid concentration in these desiccated leaves was intermediate between the undamaged and mirid-damaged leaves (5.8, 5.6, and 4.9 mg/g, for undamaged, desiccated, and mirid-damaged leaves, respectively, $P = 0.04$). In contrast, during the natural maturing and senescing process, toxic alkaloids in larkspur leaves decline to less than 1 mg/g (Pfister, unpublished data). It appears that mirid-induced senescence stops alkaloid exportation and retains the alkaloids within the leaves.

Variation in Alkaloid Concentration

There was more variation in toxic and total alkaloid concentration between larkspur plants than between mirid-damaged and undamaged parts of the same plant. Toxic alkaloid concentration varied from a low of 0.6 to a high of 6.1 mg/g in heads and from 1.1 to 12.7 mg/g in leaves. Total alkaloid concentration varied from 6.2 to 26.3 mg/g in heads and from 3.4 to 47.6 mg/g in leaves. This represents a 7- to 10-fold difference in toxic alkaloids and 4- to 14-fold difference in total alkaloids. In partitioning the source of variability in the analysis of variance in the 1995 study, 77–98% of the variation in both toxic and total alkaloids in leaves was due to differences between plants, compared to only 0.01–7% due to treatments (mirid-damaged vs. undamaged plant parts). In the heads, 51–88% of the variation was due to differences between plants, but the variation due to treatment ranged from 3 to 35%. In the 1996 study, variability due to differences between plants ranged from 47 to 91% of total variability. Clearly, most of the variation in toxic and total alkaloids occurs between plants, rather than from any mirid-induced response within a plant. This is why we compared mirid-damaged and undamaged parts on the same plant.

It is generally accepted that plants evolved chemical defenses to protect against herbivory of insects (Tallamy and Raupp, 1991) and browsing mammals (Bryant et al., 1992). However, the capacity of a plant to induce synthesis of secondary compounds is largely under genetic control (Coleman and Jones, 1991). Some plants can respond to damage and stress, while others cannot. Different genotypes may have different thresholds before inducing a response, and the response may vary in type and degree. Constitutive levels (initial levels) may vary greatly between individual plants and thus mask response to treatments.

Nutrients

Mirid-damaged larkspur leaves were lower in CP and higher in NDF than undamaged plants ($P < 0.01$, Table 2). This supports the theory that mirids are extracting cell solubles from larkspur leaves, leaving a higher proportion of fiber from the cell walls. Pfister et al. (1988b) reported that tall larkspur was a nutritious forage. Crude protein in its leaves declined from a high of 27% in early growth, to 9% at the end of the season. NDF remained between 10 and 15% throughout the season. The decline in nutrients and increase in fiber may contribute to the reduced palatability of mirid-damaged larkspur to cattle. In a previous feeding trial, cattle preferred undamaged larkspur compared to mirid-damaged larkspur (Ralphs et al., 1997a). In that study, mirids were not present on larkspur plants fed to cattle (they were shaken off when the plants were harvested), and recent rains had washed all their fecal material off the leaves.

Therefore, taste, physical texture, and nutrient quality were the only factors influencing palatability. In natural larkspur populations infested with mirids, the physical presence of mirids and the accumulated fecal material on the leaves probably would further reduce larkspur's acceptability to cattle.

CONCLUSIONS

It is readily apparent that damage from larkspur mirids did not induce norditerpenoid synthesis. Rather, there was a slight decline in toxic alkaloid concentration in larkspur leaves. Ralphs et al. (1997b,c) reported that the relative concentration of both toxic and total alkaloids increased in larkspur plants stressed by shade, photosynthesis inhibition, and herbicide treatments. They speculated that nonstructural carbohydrates and other soluble compounds declined during these stresses, thus increasing the relative concentration of a constant amount of alkaloids. The response of toxic alkaloids to feeding stress from mirids in this study was opposite. The relative concentration of toxic alkaloids declined in mirid-damaged leaves, along with a decline in N and an increase in fiber. Perhaps the mirids extracted toxic alkaloids from larkspur, thus accounting for the slight decline in concentration. Further research is being conducted to determine if the toxic norditerpenoid alkaloids are sequestered by the mirids and excreted in their fecal material. It appears that damage from larkspur mirids does not induce norditerpenoid alkaloid synthesis as a chemical defense in tall larkspur.

Even though mirids reduced toxic alkaloids in larkspur leaves, it may not have been sufficient to reduce the threat of poisoning cattle. Toxic alkaloid levels above 3 mg/g pose a threat to grazing cattle (Ralphs et al., 1997d). Only the mirids at Yampa, Colorado, reduced toxic alkaloids below the toxic threshold. It is unlikely that damage from the larkspur mirid will universally reduce larkspur toxicity below the toxic threshold. In fact, if damaged leaves senesce and retain the alkaloids, rather than translocating them out during the natural senescing process, toxicity of larkspur may be arrested at a high level. The benefit of the larkspur mirid as a biological tool rests solely in its ability to damage larkspur and render it unpalatable to cattle.

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